INTERSPECIFIC AGGRESSIVE BEHAVIOR OF THE CORALLIMORPHARIAN *CORYNACTIS CALIFORNICA* (CNIDARIA: ANTHOZOA): EFFECTS ON SYMPATRIC CORALS AND SEA ANEMONES

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ABSTRACT

Corallimorpharians are sessile cnidarians that are morphologically similar to the actiniarian sea anemones and scleractinian corals. This study describes for the first time the behavioral mechanism and effects of aggression by a corallimorpharian. Polyps of the temperate clonal corallimorpharian *Corynactis californica* extruded their mesenteries and associated filaments onto members of certain species of sea anemones and corals. They did not exhibit this behavior intraspecifically, and members of different clones of *C. californica* remained expanded upon contact. In contrast, members of four species of corals and zoanthids responded to contact with *C. californica* by contracting their tentacles, and members of three sea anemone species bent or moved away, detached from the substrate, or attacked using their aggressive structures. When interspecific contact was prolonged, individuals of *C. californica* extruded filaments onto, and killed polyps of, the sea anemones *Anthopleura elegantissima* and *Metridium senile* within 3 weeks, and the corals *Astrangia lajollaensis* and *Balanophyllia elegans* within 4–10 months under laboratory conditions. The use of extruded mesenterial filaments by *C. californica* to attack members of other anthozoan species is similar to the aggressive behavior exhibited by many scleractinian reef corals. Field observations suggest that *C. californica* may use this agonistic behavior during interspecific competition for space on hard marine substrate.

INTRODUCTION

Some of the most striking behaviors exhibited by members of the class Anthozoa (Phylum Cnidaria) are the aggressive behaviors of certain actiniarian sea anemones and scleractinian corals. Corals may attack competitors using sweeper tentacles (Richardson *et al.,* 1979; Wellington, 1980; Bak *et al.,* 1982; Chornesky, 1983; Hidaka and Yamazato, 1984), sweeper polyps (Sheppard, 1982), extruded mesenterial filaments (Lang, 1973; Glynn, 1974; Loya, 1976; Cope, 1981; Bak *et al.,* 1982; Logan, 1984), or nematocysts discharged from the colony surface (Rinkevich and Loya, 1983), and actiniarian sea anemones may use elongated catch tentacles (Williams, 1975; Purcell, 1977) or marginal vesicles called acrorhagi (Bonnin, 1964; Francis, 1973b; Ottoway, 1978; Bigger. 1980; Brace, 1981; Ayre, 1982; Sebens, 1984). These aggressive responses are complex. They often involve the induced morphogenesis and directed application of specialized structures packed with nematocysts (Purcell, 1977; Chornesky, 1983; Watson and Mariscal, 1983; Hidaka and Yamazato, 1984; Hidaka, 1985), and may be initiated upon recognition of other genotypes or species of anthozoans (Lang, 1973; Bigger, 1980).

However, little is known about the aggressive behavior of another group of antho-zoans, the corallimorpharians. Sebens (1976) reported the effects of competitive in-teractions between corallimorpharians and other anthozoans on the Caribbean coast of Panama, but did not specify the behaviors they used. The only other study relating to corallimorpharian behavior is that of Hamner and Dunn (1980), who described the unique feeding mechanism of some tropical Pacific corallimorpharians in which prey are enfolded in the oral disk.

Corallimorpharians occur throughout the world (Carlgren, 1949) and may be abundant on temperate rocky shores (Hand, 1955; Forster, 1958; Pequegnat, 1964; Castric-Fey *et al.,* 1978; Foster and Schiel, 1985), as well as on tropical coral reefs (Fishelson, 1970; den Hartog, 1980). Certain members of this group form clonal ag-gregations that cover large areas of hard substrate, and are the dominant sessile organ-isms in some temperate marine communities (Forster, 1958; Castric-Fey *et al.,* 1978). Thus, interactions of corallimorpharians with other sessile organisms may have im-portant consequences for the structure of these communities.

Corallimorpharians superficially resemble the actiniarian sea anemones in that they lack a calcareous skeleton (Carlgren, 1949). However, they are more like the stony corals in most other aspects of their morphology: they lack basilar muscles, may have tissue connections between adult polyps, lack ciliated tracts on their mesenterial filaments, and their cnidae are similar to those of corals (Carlgren, 1949; Schmidt, 1974; den Hartog, 1980). In light of the morphological relationships among members of these three anthozoan groups, a comparison of their aggressive behaviors is of interest.

This study describes the interspecific aggressive behavior of the temperate clonal corallimorpharian *Corynactis californica.* This behavior was first recorded in Chao's (1975) unpublished student paper. He observed that *C. californica* extruded mesen-terial filaments to damage the sea anemones *Anthopleura elegantissima* and *Metrid-ium senile* during interspecific interactions in the laboratory. This is aggression, which is defined by *Webster's Third New International Dictionary* as "an offensive action or attack," and in this instance is elicited upon contact with the anemones. Haderlie *et al.* (1980) briefly mentioned this behavior in their account of the natural history of *C. californica.* The present paper expands on these reports by presenting a quantitative analysis of mesenterial filament extrusion by *C. californica,* the specific-ity of this aggressive response, and its effect on the behavior and survival of some common sea anemones and corals under laboratory conditions.

Natural history

Corynactis californica Carlgren 1936 is the only species of corallimorpharian to occur along the west coast of North America, where it ranges from Washington State (Birkeland, 1971) to San Benitos Island in central Baja California (J. Engel, Tatman Foundation, pers. comm.). Members of this species reproduce asexually by fission (Hand, 1955) and budding (pers. obs.) to form aggregations on hard substrate (Fager, 1971; Haderlie *et al.,* 1980; Foster and Schiel, 1985), from the lower intertidal zone (Hand, 1955) to at least 50 meters depth (Birkeland, 1971; Schmieder, 1984, 1985). *C. californica* polyps are common on the vertical faces of subtidal rock reefs where they attain densities of up to 3000 polyps per square meter (Pequegnat, 1964). In southern California, field experiments show that the presence of aggregations of *C. californica* may increase the abundance of rock oysters (Vance, 1978) and mussels (Landenberger, 1967; Wolfson *et al.,* 1979) by protecting them from predation by sea stars. Groups of this corallimorpharian form interspecific boundaries with clones of

the sea anemones *Anthopleura elegantissima* and *Metridium senile* on artificial sub-
strates such as wharf pilings (Chao, 1975; Haderlie and Donat, 1978) and offshore oil
platforms (Carlisle *et al.,* 1964). Groups of *C. californica* also co-occur on subtidal
rock reefs in kelp forests with several species of corals, most commonly the colonial
coral *Astrangia lajollaensis* (Pequegnat, 1964) and the solitary corals *Balanophyllia
elegans* and *Paracyathus stearnsii* (Pearse and Lowry, 1974; Lewbel *et al.,* 1981; Fos-
ter and Schiel, 1985; North *et al.,* 1985).

Color varies greatly between different clonal aggregations of *C. californica.* Clones
may be red, pink, orange, or occasionally blue or purple. Members of each aggrega-
tion asexually produce polyps of the same color in both the laboratory (pers. obs.)
and the field (Turner *et al.,* 1969). Thus, color in this species appears to be genetically
controlled, and in the present study polyps from different, distinctively colored aggre-
gations were assumed to be genetically different (non-clonemates).

Materials and Methods

Collection and maintenance of organisms

Specimens of *C. californica* and the other organisms used in this study were col-
lected at four sites along the coast of central California (Table I). Laboratory experi-
ments were conducted between June 1984 and July 1986 at three facilities of the
University of California: Bodega Marine Laboratory, Joseph M. Long Marine Labo-
ratory, and in cold rooms on the Berkeley campus. Organisms were maintained in
plastic trays supplied with flowing seawater at ambient sea temperature (13–15°C),
or in closed refrigerated aquaria filled with aerated natural seawater. All tanks were
cleaned and animals fed adult brine shrimp (*Artemia salina*) weekly.

Mechanism and specificity of aggressive behavior

The first set of experiments focused on a description of mesenterial filament extru-
sion by *C. californica,* and determination of the stimuli that elicit this response. Only
fully expanded, undamaged individuals of *C. californica* were used, and all within
two weeks of collection. Polyps were brought into contact with a range of physical
and biological stimuli (Table I) to elicit extrusion. Polyps were observed continuously
for the first hour of contact, then once each hour for at least 12 h, and then intermit-
tently for several days. A different individual of *C. californica* was used for each obser-
vation; Table 1 shows the number of replicate observations with each stimulus. Data
were collected on the diameter and behavior of each polyp, occurrence of mesenterial
filament extrusion, interval from the start of contact to extrusion, duration of extru-
sion, and the origin and maximal length of any extruded filaments.

Effects of C. californica on selected anthozoans

During the above contacts between polyps of *C. californica* and seven other spe-
cies of anthozoans (Table I), data were also collected on the behavioral response of
each anthozoan. Their responses to *C. californica* were categorized as: contracted,
expanded, bent the column away, moved away on the pedal disk, detached from the
substrate, or attacked *C. californica.* During trials between *C. californica* and mobile
anthozoans such as the actiniarian sea anemones, the latter were repeatedly moved
back into contact with *C. californica* to allow adequate time for a response.

The second set of experiments examined effects of *C. californica* on the survival
of selected anthozoans over several weeks in the laboratory. To test the effect of *C.*

californica on actiniarian sea anemones, individuals of the clonal anemones *Anthopleura elegantissima* and *Metridium senile* were placed in the center of groups of *C. californica* that were attached to shells or rocks. This method prevented movement away from contact by the anemones. Control anemones were placed on rocks that were interspersed in the same tray with experimental groups, but not in contact with *C. californica*. Data were then collected on the behavior and condition of the anemones once a week for three weeks.

Effects of prolonged contact with *C. californica* also were examined in two species of scleractinian corals, *Astrangia lajollaensis* and *Balanophyllia elegans*. Individual corals were attached to glass microscope slides or shells using H. A. Calahan's Marinepoxy (Davis Instruments, San Leandro, CA 94578). This epoxy has been used on anthozoans for several years in the laboratory without apparent harm (J. S. Pearse, University of California, Santa Cruz, pers. comm.). Barnacle shells bearing aggregations of *C. californica* were broken into small bits, and each piece of shell bearing a single polyp of *C. californica* was cemented adjacent to a coral. Empty shells with no *C. californica* were glued next to other corals as controls. Experimental and control plates of corals were then intermingled in trays of seawater, and the condition and behavior of each polyp was recorded once each month for 12 months. During this time, polyps of the asexually reproducing species budded off new individuals, and each month these were counted and the degree to which they had overgrown other polyps was determined.

RESULTS

Description of aggressive behavior in C. californica

Upon contact, the tentacles of individual *C. californica* adhered to those of polyps of certain other anthozoans. Then the interacting polyps often contracted slightly and their tentacles retracted. Over the next few minutes, the two polyps went through several cycles of expansion, contact, contraction, and re-expansion. If they maintained fairly constant tentacular contact, a mass of highly convoluted mesenteries and their associated filaments eventually appeared at the mouth or through a break in the body wall of the *C. californica* polyp (Fig. 1a). These filaments were withdrawn into the coelenteron at the end of each extrusion. Of 214 *C. californica* individuals observed, most extruded filaments through the mouth (69%), through openings in the column (7%), or along the junction of column and base (24%) of the polyp. One polyp put out filaments through the tips of its tentacles. These openings in the body wall were temporary and healed soon after the mesenterial filaments were withdrawn.

C. californica individuals almost always directed filaments laterally toward the side on which they had been stimulated (in 98% of cases, n = 214). These filaments then adhered to the source of stimulation and spread over its surface. They appeared highly extensible (Fig. 1b), and if the stimulus source was pulled away, the filaments could be stretched up to four times the diameter of the polyp to which they belonged. Extruded filaments ranged in length from 1 to 42 mm (median = 3 mm). However, most polyps extruded filaments only 1–10 mm in length (91% of polyps, n = 190), or about 0.1–1.5 times polyp diameter. Extrusion length did not vary with polyp size; small (5 mm diameter) polyps often extruded filaments at least 10 mm in length, while many large (>15 mm diameter) polyps put out filaments only 2–4 mm long. Often several mesenteries with their attached filaments were extruded by a single polyp, and they frequently spread to cover the organism that was the source of stimulation.

FIGURE 1. A. Side view of extrusion of mesenterial filaments by an individual of the corallimorphar-ian *Corynactis californica* onto a contracted polyp of the actiniarian sea anemone *Metridium senile* (left). B. Top view of mesenterial filament extrusion by two polyps of *C. californica* (center) onto a retreating individual of the actiniarian sea anemone *Anthopleura elegantissima* (upper right). Photo by Galen Rowell. Note that in both photographs the filaments extend toward the actiniarians, and that in B they adhere to the anemone as it moves away. Scale bars = 1 cm.
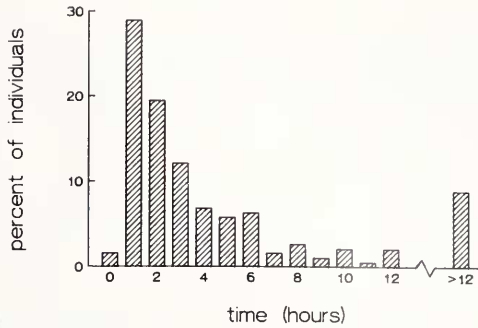
FIGURE 2. Time from start of contact to start of mesenterial filament extrusion by individuals of *Corynactis californica* upon contact with members of other anthozoan species and large food items (n = 190, median = 2.5 h, range = 0.5–72 h).

The interval from the start of contact to the start of extrusion ranged from 0.5 to 72 hours, but most individuals began to extrude filaments within a few hours of application of an appropriate stimulus (Fig. 2). At least 0.5 h of continuous contact was necessary to elicit extrusion; when contact was intermittent, extrusion often began only after several days. Most extruded filaments reached their maximal length 1–12 h from the start of contact (median = 7 h, range = 1–72 h, n = 129), and then were slowly withdrawn back into the coelenteron. The duration of extrusion varied greatly (median = 7 h, range = 1–144 h, n = 149); when contact with an appropriate stimulus was continuous, the filaments of some polyps remained extruded for up to six days.

Specificity of filament extrusion by C. californica

C. californica polyps extruded mesenterial filaments most frequently upon contact with certain types of biological stimuli (Table I). They did not respond to conspecifics, and instead, both clonemate and nonclonemate polyps remained expanded and intermingled their tentacles during contact. In contrast, a large percentage of *C. californica* individuals extruded mesenterial filaments onto members of three species of actiniarian sea anemones and the scleractinian coral *Astrangia lajollaensis* (Table I). Extrusion onto the solitary corals *Paracyathus stearnsii* and *Balanophyllia elegans* was less frequent and often occurred only after 12 or more hours of contact. All ten polyps of *C. californica* that extruded filaments onto *P. stearnsii* did so 13–50 h from the start of contact, and extrusion was observed onto *B. elegans* only after several days or weeks from the start. Few *C. californica* individuals responded to the zoanthid *Epizoanthus scotinus* (Table I).

C. californica polyps rarely used mesenterial filaments to attack other sessile organisms such as hydroids, colonial tunicates, sponges, or algae (Table I). However, they did extrude filaments onto food items that were too large to ingest (Table I). To assess the size threshold for ingestion of large food items, expanded individuals of *C. californica* were offered pieces of fish that were less than, equal to, or slightly greater than their own polyp volume (by visual estimate). The polyps injested food items that were smaller than or equal to their own volume in 38/49 cases (78%). When offered larger prey, however, they almost always extruded filaments over the food (Table I).

TABLE I

Collection sites, stimuli and percent of Corynactis californica *that extruded mesenterial filaments onto each source of stimulus*

Collection site	Stimulus	Common name	% *C. californica* that extruded filaments
	ANTHOZOANS		
BCHM	*Corynactis californica*	Corallimorpharian	
	clonemates		0 (28)
	non-clonemates		0 (40)
MB	*Anthopleura elegantissima*	Actiniarian sea anemone	97.7* (44)
MB	*Metridium senile*	Actiniarian sea anemone	89.4* (38)
B	*Epiactis prolifera*	Actiniarian sea anemone	100* (17)
H	*Astrangia lajollaensis*	Scleractinian coral	88.9* (27)
CH	*Paracyathus stearnsii*	Scleractinian coral	43.5 (23)
H	*Balanophyllia elegans*	Scleractinian coral	6.5 (31)
C	*Epizoanthus scotinus*	Zoanthid	13.6 (22)
	NON-ANTHOZOAN SESSILE ORGANISMS		
C	*Allopora californica*	Hydrocoral	23.5 (17)
C	*Garveia annulata*	Hydroid	0 (10)
H	*Acarnus erithicus*	Sponge	0 (28)
H	*Diaperoecia californica*	Bryozoan	11.1 (18)
H	*Archidistoma psammion*	Colonial tunicate	4.8 (21)
H	*Cystodytes lobata*	Colonial tunicate	13.3 (15)
H	*Rhodymenia pacifica*	Red alga	0 (21)
	LARGE FOOD ITEMS		
MB	*Mytilus edulis*	Bay mussel	100* (21)
H	*Sebastes* spp.	Rock fish	83.0* (53)
	PHYSICAL STIMULI		
—	Puncture with a glass needle**		4.8 (21)
—	Contact with a sterile glass rod		2.4 (42)

Numbers in parentheses indicate the number of polyps of *C. californica* exposed to each stimulus.

Collection sites: B = Breakwater at Doran Beach Park, Bodega Bay, Sonoma County, CA, on intertidal boulders, C = Cordell Bank, Marin County, CA, on rock pinnacles at 40–50 m depth, H = Hopkins Marine Life Refuge, Monterey County, CA, on rock reefs at 10 m depth, M = Monterey Municipal Wharf #2, Monterey County, CA, intertidally on wharf pilings.

* Responses significantly greater than those to all other stimuli, G-test for homogeneity of replicates, G = 14.08, P < .05.

** The column of each polyp of *C. californica* was punctured with a sterile glass needle, which was left in place for at least 12 h.

Differences were observed in the quality of extrusion onto food items *versus* anthozoans. When presented with large pieces of fish or mussel, most *C. californica* expanded, pressed their oral disks and tentacles onto the food, and extruded filaments out through their mouths (Table II). In contrast, when contacting anthozoans such as sea anemones or corals, *C. californica* often contracted and/or put out filaments laterally through openings in the body wall (Table II). Filaments extruded onto anthozoans also were significantly longer than those extruded onto prey items (Fig. 3).

In response to physical contact with an inert glass rod, or physical damage to the column wall, *C. californica* rarely extruded filaments (Table I). However, polyps did put out filaments when subjected to extreme physical stress, such as when they were accidentally crushed or became desiccated. Individuals also occasionally extruded filaments in the absence of any apparent stimuli.

TABLE II

Comparison of behavioral responses to different stimuli (food items versus anthozoans)
by Corynactis californica *during extrusion of mesenterial filaments*

		Number of C. californica with each type of response during extrusion			
	Posture: Filament origin:	Expanded		Contracted	
Stimulus		Mouth	Body wall	Mouth	Body wall
Large food items (fish, mussel)		63	1	1	0
Anthozoans (corals, zoanthids, sea anemones)		24	29	54	23

See Table 1 for species of stimuli used.
The distribution of the responses is dependent upon the type of stimulus contacted (R × C test of independence using G-test, G = 62.67, P < .01).

Effects of C. californica *on the behavior and survival of other anthozoans*

Contact with polyps of *C. californica* caused strong avoidance or attack responses by most of the anthozoans tested (Table III). However, conspecific *C. californica* of different genotypes (non-clonemates) did not avoid each other, and most remained expanded during contact. Non-mobile anthozoans of other species, such as scleractinian corals and zoanthids, contracted their tentacles and often their entire polyps within minutes when placed in contact with *C. californica* (Table III). Two individuals of the coral *Paracyathus stearnsii* extruded their mesenterial filaments at 7 h but these did not extend far enough to contact or damage *C. californica* polyps. The actiniarian sea anemones varied in response depending upon whether they were surrounded by *C. californica* polyps. When not surrounded, most individuals of *Anthopleura elegantissima* and *Metridium senile* bent away, moved away via pedal locomotion, or attacked the corallimorpharian (Table III). Three polyps of *A. elegantissima* inflated their specialized aggressive structures called acrorhagi and applied them to *C. californica* at 0.5–2 h. These attacks left acrorhagial peels that caused localized
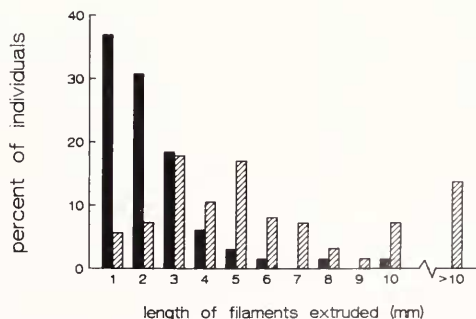

FIGURE 3. Comparison of length of mesenterial filaments extruded by *Corynactis californica* in response to large food items (shaded bars, n = 65, median = 2 mm, range = 1–10 mm) *versus* anthozoans (striped bars, n = 123, median = 5 mm, range = 1–42 mm). A significant difference exists between the two populations (normal approximation to the Wilcoson rank sum test, Z = 6.83, P < .01). See Table 1 for species used.

<div style="text-align:center">TABLE III</div>

Variation in the behavioral responses of selected anthozoans to contact with polyps of the
corallimorpharian Corynactis californica

	Total number tested	Number with each behavioral response					
Type of anthozoan		Expand	Contract	Bend away	Move away	Detach base	Attack
NON-CLONEMATE CONSPECIFICS							
OF *C. californica*	40	38	2	0	0	0	0
CORALS	106	12	92	0	0	0	2[a]
ZOANTHIDS	20	0	20	0	0	0	0
SEA ANEMONES							
Anthopleura elegantissima							
not surrounded	34	0	0	2	29	0	3[b]
surrounded	15	4	6	0	0	5	0
Metridium senile							
not surrounded	22	0	1	2	8	1	5[c] + 5[d]
surrounded	18	3	1	0	0	5	9[c]
Epiactis prolifera							
not surrounded	14	0	0	1	5	8	0

Types of attack: a = extrusion of mesenterial filaments by the coral *Paracyathus stearnsii* at 7 h; b = acrorhagi; c = extruded acontia; d = catch tentacles, used by 5/10 individuals that possessed them. See Table I for species of corals and zoanthids used.

Not surrounded/surrounded indicates whether or not each anemone was surrounded by polyps of *C. californica* during the interaction.

The distribution of responses was dependent upon the type of anthozoan involved (R × C test of independence using G-test, $P < .01$).

damage to *C. californica* polyps, but the damaged areas healed within a few days. Five out of ten polyps of *Metridium senile* that possessed well-developed aggressive structures (catch tentacles) also inflated and applied them to polyps of *C. californica* within 2–11 h of contact. However, none of these catch tentacles adhered to the corallimorpharians, and they did not appear to cause damage. *Metridium senile* also frequently extruded acontia onto *C. californica*, both when surrounded and not surrounded (Table III). The acontia adhered strongly to and killed some *C. californica* individuals. Polyps of the actiniarian sea anemone *Epiactis prolifera* were tested only when not surrounded, and most avoided contact within 3 h by moving away on the substrate or detaching their pedal disks and then rolling or floating away (Table III).

Individuals of the sea anemones *M. senile* and *A. elegantissima* were killed within one to three weeks (Fig. 4a) during prolonged contacts with surrounding groups of *C. californica* polyps. These anemones often detached from the substrate, but adhered to the tentacles of the surrounding *C. californica* polyps and were unable to escape. They were then repeatedly attacked by the extruded mesenterial filaments of *C. californica*, and their tissues became necrotic within a few days. Control anemones that did not contact *C. californica* remained expanded and firmly attached to the substrate throughout the experiment.

Corynactis californica had a much slower but fatal effect on members of two species of scleractinian corals. Within two weeks from initial contact, *C. californica* had caused tissue damage to most individuals of the corals *Astrangia lajollensis* (57/74 polyps damaged, =77%), and *Balanophyllia elegans* (12/19 polyps damaged, =63%).
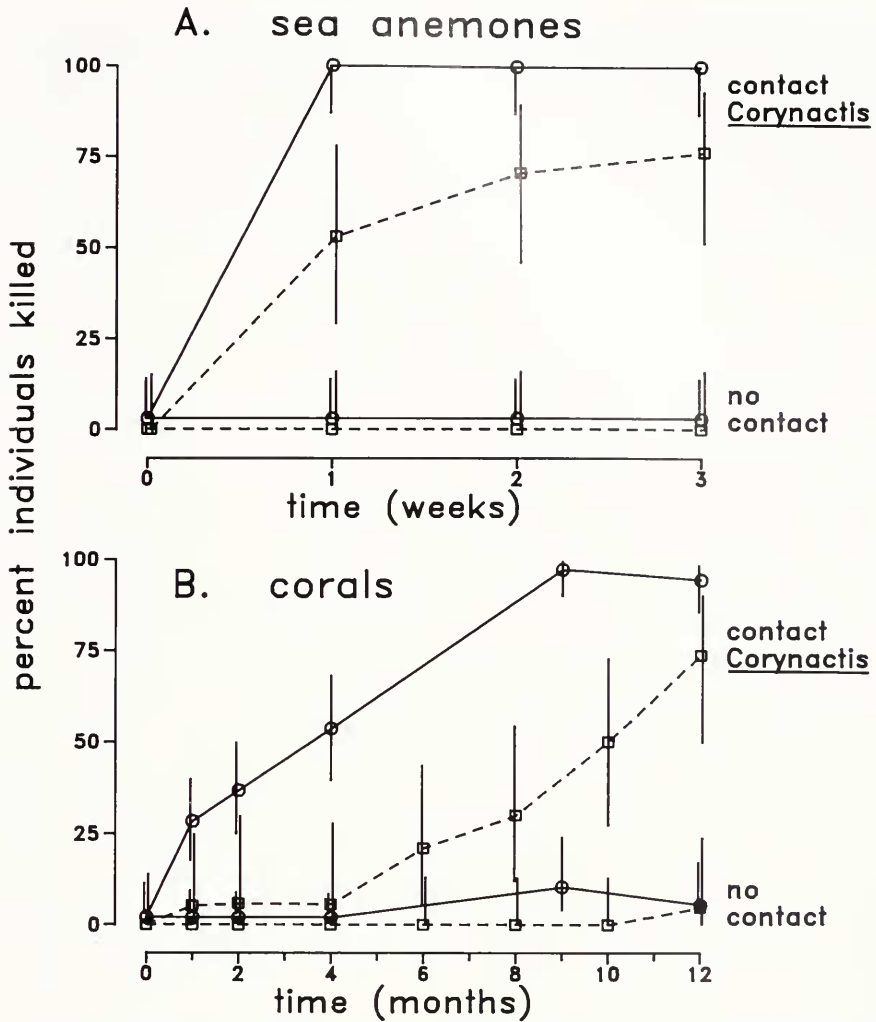
A. sea anemones

B. corals

FIGURE 4.   Effect of contact with the corallimorpharian *Corynactis californica* on the survival of selected sea anemones and corals. Bars represent 95% confidence limits. See text for details. A. Effect on polyps of the actiniarian sea anemones *Anthopleura elegantissima* (solid lines, n = 21 contact, n = 20 no-contact) and *Metridium senile* (dashed lines, n = 17 contact, n = 17 no-contact). At three weeks, the proportions of anemones killed in the experimental (contact) *versus* control (no-contact) groups were significantly different for both species (G-test of independence for proportions, $P < .01$). B. Effect on polyps of the scleractinian corals *Astrangia lajollaensis* (solid lines, n = 69 contact, n = 31 no-contact) and *Balanophyllia elegans* (dashed lines, n = 19 contact, n = 21 no-contact). At twelve months the proportions of corals killed in the experimental (contact) *versus* control (no-contact) groups were significantly different for both species (G-test of independence for proportions, $P < .01$).

During the ensuing months, *C. californica* polyps asexually produced many new individuals which eventually grew over and around the corals. In 6 months on one plate, 10 *C. californica* individuals produced over 80 polyps that killed and covered the original 10 *A. lajollaensis* polyps. After 12 months of contact, corallimorpharian polyps had killed most of the corals on the experimental plates (Fig. 4b).

C. californica individuals appeared to affect only the corals that they touched. In several cases, tissue was damaged and calcareous skeleton was exposed only on the side of a coral that faced toward a *C. californica* polyp. In cases where asexually produced polyps of *C. californica* grew away from and ceased to contact the experimental corals, the latter remained healthy and undamaged. Control corals that were isolated from contact with *C. californica* also remained alive (Fig. 4b), and during the year produced many new polyps, presumably both sexually (via brooded planulae) in *Balanophyllia elegans,* and asexually (via clonal budding) in *Astrangia lajollaensis.*

DISCUSSION

This report is the first detailed description of aggressive behavior in a corallimorpharian. The type of aggression exhibited by *C. californica,* extrusion of mesenterial filaments, is very similar to the attack behavior of many tropical scleractinian corals (Lang, 1973; Glynn, 1974; Loya, 1976; Wellington, 1980; Cope, 1981; Bak *et al.,* 1982; Logan, 1984). *C. californica* and certain corals readily extrude their mesenterial filaments onto members of other anthozoan species and onto large food items (Table I; Yonge, 1930a; Lang, 1973). The timing of the extrusion response is also remarkably similar in corals and *C. californica.* Lang (1973) reported that Jamaican reef corals extruded their filaments 0.5–12 h after initiation of contact with certain coral species, and Glynn (1974) noticed extrusion by eastern Pacific corals 8–12 h after contact with competing corals. In the present study, most *C. californica* individuals also put out their filaments within 12 h (Fig. 2). The extruded filaments of both *C. californica* and scleractinian corals cause extensive damage to and eventually kill other anthozoans if contact is prolonged and if, in corals, the other colony is small enough (Lang, 1973; Fig 4). Since corals and corallimorpharians are morphologically very similar (den Hartog, 1980), one might expect to see this similarity in their aggressive behaviors as well. This type of aggression, via mesenterial filament extrusion, differs from the competitive behavior of some of the actiniarian sea anemones that coexist with *C. californica* and use their marginal spherules (Francis, 1973b) or catch tentacles (Purcell, 1977) to attack competitors. These differences in behavior underscore the major morphological differences between a corallimorpharian such as *C. californica,* and actiniarian sea anemones. They also support the idea that corallimorpharians are more closely related to scleractinian corals than they are to sea anemones.

Unlike the specialized aggressive structures of actiniarian sea anemones that are used only during competitive interactions (Bonnin, 1964; Francis, 1973b; Williams, 1975; Purcell, 1977; Watson and Mariscal, 1983), the mesenterial filaments of *C. californica* appear to serve a variety of functions. In all anthozoans studied thus far, the mesenterial filaments are the major sites for digestion and absorption of food in the coelenteron (Yonge, 1930b; Nicol, 1959; Van-Praet, 1985). These filaments contain gland cells that secrete strong proteolytic enzymes, as well as nematocysts that may inject cytolytic toxins into prey (Van-Praet, 1985). Special areas on the filaments and adjacent mesenteries then absorb the partially digested foodstuffs (Yonge, 1930b; Van-Praet, 1985). *Corynactis californica* also extrudes mesenterial filaments onto food that is too large to take into the coelenteron (Table I), presumably to digest it externally. This behavior allows polyps to consume a large range of prey sizes. Certain tropical Pacific corallimorpharians envelope prey in the oral disk, and then extrude filaments out of the mouth to digest them (Hamner and Dunn, 1980). Many species of reef-building corals also consume prey externally via extruded filaments (Carpenter, 1910; Yonge, 1930a, 1968; Goreau *et al.,* 1971). Thus, two major functions of

mesenterial filaments in these organisms appear to be the internal breakdown and absorption of food, and external consumption of large prey. Mesenterial filaments also are used during physical stress. Some corals extrude their filaments when oil is introduced into their coelenterons (Bak and Elgershuizen, 1976), when they are exposed to intense light (Lang, 1973), or when they are handled roughly (Duerden, 1902). *C. californica* polyps also exhibit extrusion when stressed (see Results). Finally, divers observed *C. californica* polyps extruding their mesenterial filaments onto one of their major predators, the sea star *Dermasterias imbricata* (Annett and Pierotti, 1984; pers. obs.). Thus, the lobed filaments along the edges of anthozoan mesenteries may serve multiple functions in certain corals and corallimorpharians.

An interesting aspect of the aggressive/defensive use of mesenterial filaments by *C. californica* is the complete lack of response to conspecifics (Table I). Members of a given clonal aggregation presumably would benefit from damaging and overgrowing those of a different, genetically distinct aggregation (as discussed by Francis, 1973b). However, in the field distinctly colored groups of *C. californica* often intermingle and show no evidence of aggression or damage along their interacting borders (pers. obs.). The wide, anemone-free zones that are visible between aggregations in other species known to show interclonal aggression (Francis, 1973a; Purcell, 1977) do not occur in this species. Most reef corals that use mesenterial filaments to attack competitors also only extrude them interspecifically (Lang, 1973; Cope, 1981). One exception has been reported: the Caribbean coral *Montastrea annularis* appears to extrude filaments onto conspecific colonies to damage them (Logan 1984, 1986).

The present study demonstrates that under laboratory conditions *C. californica* strongly affects both the behavior and survival of certain other anthozoans (Table III, Fig. 4). These results have several ecological implications. In shallow subtidal habitats along the coast of California where *C. californica* occurs, hard surfaces are often completely covered with organisms (Pequegnat, 1964; Haderlie and Donat, 1978; Vance, 1978; Schmieder, 1984, 1985), and space for settlement and growth may be a limiting resource for sessile animals. The species of sea anemones tested in this study often moved away from or otherwise avoided contact with *C. californica* (Table III); where they co-occur in the field, this behavior might free space for growth along the interspecific borders of *C. californica* aggregations. The avoidance responses of these sea anemones are the same behaviors used to effectively escape attack by conspecifics (Francis, 1973b; Purcell, 1977) and predators (Waters, 1973; Edmunds *et al.*, 1976). However, the specialized aggressive structures of *Anthopleura elegantissima* and *Metridium senile* apparently were not effective against *C. californica* (see Results). The acontia of *M. senile* caused the most damage to *C. californica*, and in the field may allow the former to kill polyps of the latter along their interacting borders. L. Harris (University of New Hampshire, pers. comm.) has observed that, in the laboratory, *M. senile* also uses acontia to attack individuals of the sea anemones *A. elegantissima, Actinia equina*, and *Urticina (=Tealia) piscivora*.

The results of the present study differ somewhat from those presented by Chao (1975). He described an aggressive hierarchy in which *C. californica* was dominant over *A. elegantissima*, while *M. senile* was dominant over both of the former species. The present results confirm that *C. californica* causes tissue damage to *A. elegantissima* (Table III, Fig. 4a), but show that *C. californica* and *M. senile* damage each other, with no clear competitive outcome. A clear dominance ranking of these three cnidarian species remains to be determined.

Field observations also suggest that *C. californica* damages sea anemones and corals under natural conditions. Chao (1975) noticed that interspecific boundary areas about 2–3 cm wide occurred between aggregations of *C. californica* and the sea anem-

ones *Anthopleura elegantissima* and *Metridium senile* found on intertidal pilings at the Monterey Wharf. Francis (1973b) and Purcell (1977) showed that anemone-free zones between groups within the latter two species are maintained by aggression between clones. The corridors along their boundaries with *C. californica* could be maintained by the avoidance behaviors of the anemones (Table III), or by the death of anemones that have been repeatedly attacked by the mesenterial filaments of *C. californica* (Fig. 4a).

On subtidal rock reefs, certain scleractinian corals also appear to be negatively affected by contact with *C. californica.* Fadlallah (1981) observed a polyp of *C. californica* extruding filaments onto and killing an individual of the solitary coral *Balanophyllia elegans* in the kelp forest at Hopkins Marine Life Refuge (HMLR) in Monterey. Polyps of *B. elegans* and the colonial coral *Astrangia lajollaensis* that occur adjacent to *C. californica* on subtidal boulders at HMLR often show damaged tissues and exposed skeletons (pers. obs.). In addition, the vertical distribution of *C. californica* and *A. lajollaensis* on large subtidal reefs suggests some sort of negative interaction. Pequegnat (1964) found that *C. californica* was most abundant near the top of a subtidal reef in southern California, and became more sparse with depth. In contrast, *A. lajollaensis* formed large colonies near the base of the reef and decreased in abundance with height, occurring at low densities near the reef top. These inverse patterns of abundance also can be observed on large (2–5 m high) subtidal reefs at HMLR in central California (pers. obs.). Efforts are currently underway to document the distributions of these anthozoans at HMLR, and to test the ecological effects of their behavioral interactions in the field.

Members of the genus *Corynactis* produce clonal aggregations in tropical and temperate marine habitats throughout the world (Carlgren, 1949). *Corynactis viridis* is the most abundant sessile organism on shallow subtidal rocks walls at the Glenan Archipelago on the Atlantic coast of France (Castric-Fey *et al.,* 1978), and at Plymouth, England (Forster, 1958); *C. parvula* occurs on Caribbean reefs where it may interact with a variety of corals and sea anemones (den Hartog, 1980). These congeners may show aggressive behavior similar to that of *C. californica,* as well as use other competitive mechanisms (den Hartog, 1977), thus affecting the abundance and distribution of co-occuring sessile organisms.

Many so-called lower animals exhibit complex aggressive behaviors associated with resource defense. Such behaviors are observed in polychaete worms (Evans, 1973; Dimock, 1974; Roe, 1975), chitons (Chelazzi *et al.,* 1983), limpets (Stimson, 1970; Branch, 1975; Wright, 1982), sea urchins (Schroeter, 1978; Maier and Roe, 1983), and sea stars (Menge and Menge, 1974; Wobber, 1975), as well as in the many anthozoans discussed in this paper. Yet the behaviors of these organisms are rarely considered in theoretical works on aggression and territoriality, most of which focus on birds and mammals (Waser and Wiley, 1979; Murray, 1981; Davies and Houston, 1984), nor are they included in recent texts on animal behavior (Huntingford, 1984; Ridley, 1986). Because marine invertebrates often are sessile or slow-moving, and may be clonal as well, their aggressive behaviors have developed under a different set of constraints than have those of most vertebrates. More extensive consideration of aggression in the lower invertebrates may lead to important new insights into the evolution and ecology of animal conflict.

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